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BIONOMICS OF LARVAL POPULATIONS OF *ANOPHELES PSEUDOPUNCTIPENNIS* IN THE TAPACHULA FOOTHILLS AREA, SOUTHERN MEXICO

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ABSTRACT. The population dynamics of *Anopheles pseudopunctipennis* larvae were studied in a foothill region near Tapachula, Mexico. Systematic surveillance of wet-season and dry-season habitats was conducted during 1990 and 1991. Sampling along transects of the Coatan River was employed to quantify habitat availability and population densities of larvae during the dry season. During the wet season, larvae were most abundant in temporary habitats, such as seepage springs, rain pools, and pools in stream and river margins. The temporary habitats disappeared during the dry season, which occurred concurrent with increasing densities of larvae in dry-season habitats within transects along the Coatan River. The great abundance of the dry-season riverine habitats, *viz.*, small pools with filamentous algae, resulted in peak densities of host-seeking adult populations in villages associated with the river. During both seasons, there were significant associations between the presence and abundance of larvae and habitats containing filamentous algae, and secondarily with selected aquatic and semiaquatic plants. There was a significant correlation between mean numbers of larvae per habitat and mean numbers of breeding sites in the transects. Overall, *An. pseudopunctipennis* larvae were very abundant during the dry season and relatively uncommon during the wet season.

INTRODUCTION

Anopheles pseudopunctipennis Theobald is the most widely distributed malaria vector in Mexico and an important vector in several other countries, including Guatemala, Honduras, Ecuador, Peru, and Bolivia (Pan American Health Organization 1991). This species and the coastal dweller, *Anopheles albimanus* Wiedemann, have been the main targets of the National Malaria Control Program in Mexico during the last 2 decades (Rodriguez and Loyola 1989).

Anopheles pseudopunctipennis generally inhabits areas of higher altitude, over 200 m above sea level, throughout its geographical range. This species is found from the southern United States to northern Argentina and is generally associated with mountain ranges such as the Sierra Madre in Mexico and the Andes in South America (Aitken 1945). Formation of larval breeding sites in this rugged topography is regulated by annual local rainfall patterns. When the wet season ends, larval habitats are formed by pools, ponds, and lagoons developing in the margins of rivers and streams. Floating plants and mats of filamentous algae are characteristic of these larval habitats (Hoffmann and Samano 1938, Savage et al. 1990).

Despite the usefulness of control measures directed against larvae of malaria vectors, most malaria control programs worldwide have relied heavily on the use of residual insecticides to control adult mosquitoes (Service 1976). Investigations on the ecology and biology of the larvae of *An. pseudopunctipennis* and other vectors have been performed infrequently. Included here are observations on the bionomics of the larval stages of *An. pseudopunctipennis* including seasonal changes in larval abundance and the seasonal dynamics of larval habitats in a malarious area of southern Mexico.

MATERIALS AND METHODS

Study area: Study sites were located between 300 and 650 m above sea level in a hilly area, which is part of the West Sierra Madre Mountain range, near the city of Tapachula in southern Mexico. The Coatan River, one of the largest in the mountain range, cuts across about 16 km of the foothill region. Four villages near the river, El Retiro, El Plan, La Ceiba, and La Concordia, were selected as study sites. Seasonal vivax malaria occurs in the 4 villages.

The region is mostly devoted to coffee production and, secondarily, to banana and cacao cultivation. Although the natural vegetation is continuously being replaced by coffee plantations, remnants of a deciduous tropical forest still exist. The average annual rainfall of 3,800 mm is distributed mostly within a 6-month wet season, from May to November, and is followed by a dry season from December through April. Average annual temperature is 25°C, and relative humidity is 80–90% for most of the year.

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Topography varies from gentle slopes to very steep hills and mountains, and narrow valleys. A large number of creeks, streams, seepage springs, and temporary roadside puddles are present during the wet season. Some of these habitats support anopheline breeding; however, only lagoons, reservoirs, man-made gravel pits, and some large ground pools contain water throughout the year.

Water of the Coatan River has been used by the hydroelectric plant, "Cecilio de Valle", for the last 20 years. The water is collected 1 km upstream from El Retiro, the highest study site, channeled into a tube leading into a reservoir at the hydroelectric plant, and dumped back into the Coatan River at a site upstream from La Concordia village, the lowest study site. Environmental conditions created by this diversion of water result in abundant *An. pseudopunctipennis* breeding sites along margins of the river from late December to early May, during the dry season.[4]

Wet-season larval habitats: During the wet season of 1990, mosquito larval habitats located in villages and coffee plantations throughout the study area were surveyed. Flood pools in margins of creeks, streams, rivers, irrigation canals, and springs, as well as lagoons, rain puddles, ponds, reservoirs, dams, ground pools, and gravel pits were surveyed for the presence of larvae. At each of these sites, larvae were collected with 30 dips, using standard 350-ml dippers (Service 1976). During the first site visit, larvae were collected and taken to the Centro de Investigación de Paludismo (CIP) insectary where they were reared to adults and identified (Wilkerson et al. 1990). To prevent possible confusion with anopheline species other than *An. pseudopunctipennis* that might be present in selected sites, a few sites initially found to harbor other *Anopheles* species were eliminated from the study, and only *An. pseudopunctipennis* and anopheline-negative sites were selected and monitored. Selected sites were visited either fortnightly or monthly during the next 12 months. Larvae were collected, counted, and returned to their breeding site to avoid population disturbances that might affect the larval densities.

The wet-season habitats of *An. pseudopunctipennis* larvae were classified using criteria established by Rejmankova et al. (1991). Estimates of larval productivity for each category of habitat were based on the percentage of total collections positive for larvae and the mean density of larvae/dip. Additionally, the following statistics were calculated from the surveillance data: 1) percentage of visits that were positive for larvae over all sampling visits, 2) percentage of visits when a wet-season category of habitat contained water over the total number of visits, and 3) percentage of visits when habitats of a given category contained water during the dry-season visits. Wet-season sites were considered positive if more than one specimen was collected during more than one visit.

Habitats were characterized by collecting and identifying aquatic and semiaquatic plants from each habitat (Miranda 1952). Filamentous algae were recorded as present or absent at each site. Temporal associations between larval abundance and algae and plant populations for each category of wet-season larval habitat were analyzed by the Fisher exact, 2-tailed test (Zar 1984).

Dry-season larval habitats: During the dry season, surveillance of transects along the Coatan River was used to quantify numbers of pools produced and larval densities at locations near each of the 4 villages. Pools were produced at the edges and in the rocky bed of the river as a consequence of diminished water flow during the dry season. A transect consisted of a linear distance of 200 m along both sides of the river, including the river bed. Distances between transects and village sites were about 1 km to El Retiro, 0.5 km to El Plan, 2 km to La Ceiba, and 1 km to La Concordia.

Transects were sampled at 2-week to 1-month intervals. Sampling began at the end of the wet season, in November 1990, and was continued throughout the dry season, until June 1991. Larvae were collected with a standard 350-ml dipper, and 10 dips were made at each potential breeding site (river pool). Samples of 5–10 field-collected specimens were taken to the CIP for identification; most larvae were returned immediately to the collection sites.

Changes in larval densities were estimated by the mean numbers of larvae per dip, and the number of available dry-season habitats/transect/month. The Pearson correlation coefficient and simple linear regression analyses tested for associations between densities of larvae and numbers of dry-season larval habitats, between larval abundance and percentage of surface area with filamentous algae, and between larval density and size of habitat (SYSTAT 1989). The numbers of larval habitats in different transects were compared by the nonparametric Wilcoxon rank test (Siegel 1956). Additionally, the monthly average number of larvae per square meter of filamentous algae was estimated by taking the total number of larvae collected in all pools with-

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[4] Fernandez-Salas, I. 1992. Bionomics of the primary malaria vector, *Anopheles pseudopunctipennis* in the Tapachula foothill area of southern Mexico. Ph.D. dissertation. USUHS, Bethesda, MD.

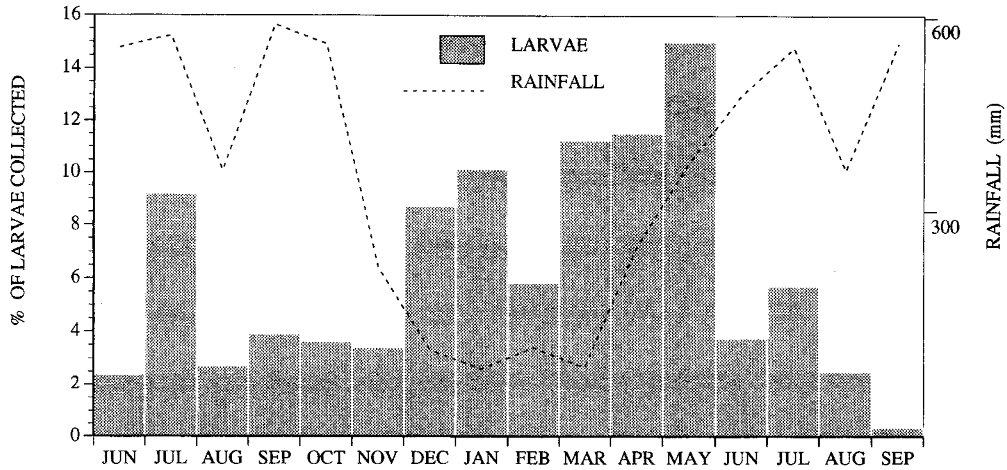

Fig. 1. Abundance of *Anopheles pseudopunctipennis* larvae in wet-season habitats vs. amount of rainfall per month in the foothills near Tapachula, Mexico. Percentage of larvae collected are plotted by month from June 1990 to September 1991. Numbers of larvae compiled by continuously monitoring wet-season habitats.

in a transect divided by the total surface area of filamentous algae for all pools for each month. The length and width of patches of filamentous algae were measured by a tape measure. These measurements were then used to calculate an estimate of square surface area of larval habitat.

Usefulness of larval surveillance as an estimator of adult densities in study villages was evaluated by correlation coefficients of monthly densities of larval and adult populations. Data on monthly means of adult relative abundances consisted of pooled indoor and outdoor collections of adult *An. pseudopunctipennis* females as they landed on human hosts (Fernandez-Salas et al. 1994). The numbers of larvae and adults were transformed to $\log(x + 1)$ (Service 1976) for the analyses.

RESULTS

Wet season larval habitats: Larval abundance in the study area was negatively associated with annual rainfall (Fig. 1). Maximum larval abundance occurred during the dry season and larval abundance was least during the wet season. A group of 75 mosquito larval habitats was surveyed in the wet season of 1990. Ten sites were identified as *An. albimanus* and *Anopheles apicimacula* Dyar and Knab habitats and were eliminated from surveillance. Almost 70.0% of the wet season sites were transitory, consisting of rain puddles (26.2%), streams (17.0%), seepage springs (12.3%), and flood pools in river margins (12.3%) (Table 2). These transitory habitats produced more than two-thirds (70.1%) of the total numbers of larvae collected during the wet season. Seepage springs produced the largest numbers of larvae (25.1%), followed by ponds (21.9%), rain puddles (15.2%), river margin pools (15.1%), and streams (14.7%). Lagoons, gravel pits, and reservoirs produced relatively few *An. pseudopunctipennis* larvae (Table 1).

Fifty-one (78.5%) (Table 2) wet season habitats were positive for *An. pseudopunctipennis* larvae during 13.2–56.6% of all sampling visits (Table 1). Pools associated with seepage springs and flooded river margins were most frequently positive for *An. pseudopunctipennis* larvae during sampling visits (56.6 and 40.0%, respectively). These results were based on 12 continuous months of surveillance. Rain puddles and gravel pits were less frequently positive for larvae (22.5 and 13.2%, respectively) (Table 1). Habitat availability from wet to dry season varied drastically for some favored habitats (e.g., seepage springs were available during 83.0% of all wet season visits, but were available for only 11.8% of the dry season visits). Similar reductions in availability of wet-season habitats were documented for rain puddles (87.4 to 18.0%), flood pools in river margins (90.3% to zero), and streams (91.0 to 25.0%). Larger bodies of water, such as ponds, large lagoons, and gravel pits, were not heavily affected by seasonal changes, and were available throughout the year.

Filamentous algae, mostly species of *Spyrogira* and *Oedogonium* (Prescott 1978), were found in 46.2% of all wet season habitats, and in 59.0% of the habitats that were positive for larvae (Table 2). Filamentous algae were significantly as-

Table 1. Habitat availability and relative numbers of *Anopheles pseudopunctipennis* larvae produced by different categories of aquatic habitats in the foothills near Tapachula, Mexico, from June 1990 to September 1991.

Category of habitat	*n*	% larvae by habitat	No. of visits[1]	% visits[2] positive for larvae	% of wet-season visits with water in habitats (number)[3]	% of dry-season visits with water in habitat (number)[4]	Mean no. larvae per dip in wet season[5]	Mean no. larvae per dip in dry season[6]
Springs	8	25.1	76	56.6 (43)	83.0 (63)	11.8 (9)	0.70	0.68
Ponds	9	21.9	141	30.5 (43)	98.0 (138)	100 (141)	0.48	0.79
Rain puddles	17	15.2	111	22.5 (25)	87.4 (97)	18.0 (20)	0.38	1.12
River flood pools	8	15.1	93	40.0 (37)	90.3 (84)	0.0 (0)	0.41	0.34
Streams	11	14.7	132	24.0 (31)	91.0 (120)	25.0 (33)	0.29	1.29
Lagoons	8	6.9	97	25.0 (24)	93.8 (91)	87.6 (85)	0.25	0.62
Gravel pits	3	0.5	38	13.2 (5)	97.4 (37)	65.7 (25)	0.12	0.20
Reservoir	1	0.5	16	25.0 (4)	100 (16)	100 (16)	0.12	4.66
Totals	65	99.9						

[1] Pooled monthly or fortnightly habitat sampling.
[2] Larvae were found.
[3] Times habitat had water in wet season/total sampling visits.
[4] Times habitat had water in dry season/total sampling visits.
[5] Total number of larvae/number of positive visits in the wet season/number of dips per visit (30).
[6] Total number of larvae/number of positive visits in the dry season/number of dips per visit (30).

sociated with seepage springs (Fisher exact test, $P < 0.05$). A high percentage (72.7%) of streams also contained filamentous algae. Positive associations were also documented for *Ludwigia octovalvis* and *Panicum* spp. with flood river margin pools, *Heteranthera limosa* with seepage springs, and *Eichhornia crassipes* and *Pistia stratiotes* with ponds. Weaker associations were found between the presence of *An. pseudopunctipennis* larvae and *Heterantera limosa, Ludwigia octovalvis,* and *Paspalum* sp. (Fisher exact, 2-tailed test, $P < 0.10$).

Dry season larval habitats: The numbers of pools and patches of filamentous algae along transects of the Coatan River during the dry season were negatively related to rainfall (Fig. 2). The annual rainfall pattern consisted of diminishing rain in November, followed by low amounts of rainfall from December through March. Rainfall started to increase in late April, followed by heavy rains in May. Isolated river pools with *An. pseudopunctipennis* larvae began to appear in November. These habitats continued to increase in number throughout the dry season but were washed away by increased water flow in May.

Overall, the largest numbers of larval habitats were recorded for transects at El Retiro and El Plan, with means of 56.1 and 57.1 habitats per transect, respectively. Fewer habitats formed along the transect at La Ceiba, with a mean of 24.8 pools. The least number of habitats was recorded for the transect at La Concordia, with a mean of 0.7 per transect. There were no differences in numbers of habitats between El Retiro and El Plan (Wilcoxon rank test, $P > 0.05$), but these 2 sites were statistically different from La Ceiba and La Concordia ($P < 0.05$).

Anopheles pseudopunctipennis larvae appeared quickly as habitats formed in the transects. The percentages of such habitats with *An. pseudopunctipennis* larvae varied from 64.4 to 76.6%. There was a clear and direct relationship (as defined by linear regression analysis) between the monthly numbers of larval habitats and average densities of larvae for transects at El Retiro ($r = 0.66$, $\beta = 0.015$, $P = 0.13$), El Plan ($r = 0.58$, $\beta = 0.011$, $P = 0.04$), and La Ceiba ($r = 0.555$, $\beta = 0.023$, $P = 0.05$). This relationship was not detectable with data from La Concordia.

The presence of filamentous algae was a consistent characteristic of the riverine larval habitats during the dry season. Several genera of filamentous algae belonging to the phylum Chlorophyta grew in the sunny pools. *Spirogyra, Chladophora, Oedogonium,* and *Closterium* comprised the 4 most prevalent genera. Two species of the first genus were collected most frequently, *viz., S. malmeara* and *S. mayuscula* (Prescott 1978). Filamentous algae were consistently present in the 4 transects. The lowest mean percentage of algae and pool associations recorded was for La Ceiba (62.5%) and the highest was in La Concordia (83.3%). Data from the 2

Table 2. Associations of *Anopheles pseudopunctipennis* larvae with plants in different categories of wet-season habitats that were sampled in the foothills near Tapachula, Mexico, from June 1990 to September 1991.

Associated taxa	Categories of wet-season larval sites								
	Rain puddles	Streams	Ponds	Springs	Lagoons	River flood pools	Gravel pits	Reservoir	Totals
	17 (26.2)[1]	11 (17.0)	9 (13.8)	8 (12.3)	8 (12.3)	8 (12.3)	3 (4.6)	1 (1.5)	65 (100)
An. pseudopunctipennis	8 (47.1)[2]	10 (91.0)	7 (77.8)	8 (100)	7 (87.5)	7 (87.5)	3 (100)	1 (100)	51 (78.5)
Filamentous algae	6 (35.3)	8 (72.7)	4 (44.4)	8 (100)[3]	2 (25.0)	2 (25.0)	—[4]	—	30 (46.2)
Plants									
Paspalum sp.	9 (53.0)	4 (36.4)	5 (55.6)	1 (12.5)	2 (25.0)	3 (37.5)	2 (66.7)	1 (100)	27 (41.5)
Ludwigia octovalvis	3 (17.6)	4 (36.4)	—	3 (37.5)	2 (25.0)	5 (62.5)[3]	—	—	17 (26.2)
Cyperus sp.	3 (17.6)	3 (27.3)	1 (11.1)	—	3 (37.5)	3 (37.5)	1 (33.3)	—	14 (21.5)
Heteranthera limosa	4 (23.5)	1 (9.1)	—	4 (50.0)[3]	—	—	—	—	9 (13.8)
Panicum sp.	1 (6.0)	—	1 (11.1)	—	1 (12.5)	3 (37.5)[3]	—	1 (100)	7 (10.8)
Commelina sp.	1 (6.0)	3 (27.3)	1 (11.1)	1 (12.5)	—	—	1 (33.3)	—	7 (10.8)
Mimosa sp.	3 (17.6)	—	—	—	—	—	3 (100)	—	6 (9.2)
Echinochloa colonum	2 (11.8)	—	—	2 (25.0)	1 (12.5)	1 (12.5)	—	—	6 (9.2)
Eichhornia crassipes	—	—	3 (33.3)[3]	—	1 (12.5)	—	—	—	4 (6.2)
Pistia stratiotes	—	—	3 (33.3)[3]	—	1 (12.5)	—	—	—	4 (6.2)
Oryza latifolia	—	1 (9.1)	—	—	2 (25.0)	—	—	—	3 (4.6)
Ipomoea sp.	—	—	—	1 (12.5)	1 (12.5)	—	—	—	2 (3.1)
Podostemaceae	—	—	—	—	2 (25.0)	—	—	—	2 (3.1)
Fimbristylis sp.	1 (6.0)	—	—	1 (12.5)	—	—	—	—	2 (3.1)
Veronica cf. *peregrina*	1 (6.0)	1 (9.1)	—	—	—	—	—	—	2 (3.1)
Cynodon dactylon	2 (11.8)	—	—	—	—	—	—	—	2 (3.1)
Dichronema sp.	1 (6.0)	—	1 (11.1)	—	—	—	—	—	2 (3.1)
Heliconia sp.	1 (6.0)	1 (9.1)	—	—	—	—	—	—	2 (3.1)
Pennisetum sp.	1 (6.0)	—	—	—	—	—	—	—	1 (1.5)
Bulbostylis sp.	—	1 (0.0)	—	—	—	—	—	—	1 (1.5)
Typha domingensis	—	-	1 (11.1)	—	—	—	—	—	1 (1.5)

[1] Number of sites and percent of all available categories of breeding sites.
[2] Number of positive sites (%).
[3] $P < 0.05$, Fisher exact test, 2 tails.
— Not found.

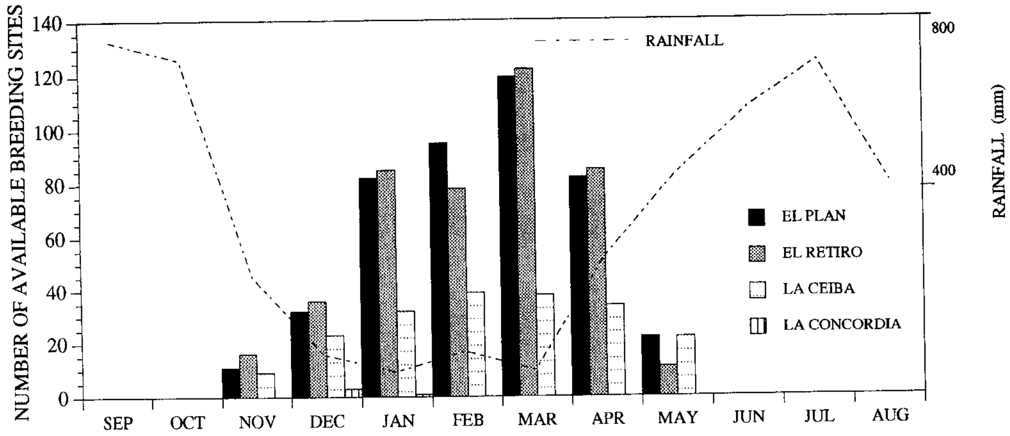

Fig. 2. Pattern of monthly rainfall vs. total numbers of *Anopheles pseudopunctipennis* dry season larval habitats in 4 transects along the Coatan River in the foothills near Tapachula, Mexico (September 1990 to August 1991).

transects showing the highest numbers, El Plan and El Retiro, were used to define significant ecological relationships between presence of larvae and presence of filamentous algae ($\chi^2 = 29.83$, df = 1, $P < 0.01$). Larval densities were positively associated with the percentage of surface area covered by filamentous algae ($r = 0.74$, $\beta = 0.422$, $P = 0.0001$). Larger numbers of habitats with filamentous algae occurred from January to March. A mean of 33.0 larvae/m^2 of filamentous algae were collected in El Retiro, compared to means of 28.6, 16.7, and 53.9 for El Plan, La Ceiba, and La Concordia, respectively. The average size of habitats (m^2 of surface area) during the dry season was similar for El Retiro, El Plan, and La Ceiba, with range limits of 1.1–1.9 m^2. On average, the few habitats in the transect at La Concordia were smaller.

Pearson correlation coefficients of monthly densities of larvae vs. numbers of *An. pseudopunctipennis* adults were significant only for data from El Plan ($r = 0.68$, $P < 0.05$). Nevertheless, the abundance of adults and larvae were similar in each of the villages, with high larval densities corresponding to high adult populations (Fig. 3).

DISCUSSION

A distinct seasonality in types and availability of habitats for larvae of *An. pseudopunctipennis* was documented in 12 months of collection data. During the wet season, 70.1% of the larvae were collected from rainfall-dependent habitats, such as rain puddles, seepage springs, streams, and flood pools in river margins. Smaller numbers of larvae were collected from the more permanent ponds, lagoons, and reservoirs (Table 1). As rainfall diminished during the dry season most of the transient water bodies dried out. However, there was a concurrent increase in numbers of optimal breeding sites along several kilometers of the Coatan River as the flow of water decreased during the dry season. Population densities of *An. pseudopunctipennis* larvae and adults, and malaria transmission rates were at peak levels during the dry season (M. H. Rodriguez, unpublished data) (Fig. 3). Such rain-dependent seasonal changes in vector abundance have been documented for other mosquito species and other groups of insects in the tropics with wet–dry seasonal cycles (Wolda and Galindo 1981).

Seepage springs were relatively common in the foothills during the wet season, when they were important breeding sites and produced the largest numbers of larvae. In total, 56.6% of all the sampling visits to seepage spring habitats were positive for *An. pseudopunctipennis* larvae, including both wet and dry seasons (Table 1). This important relationship has also been documented for this anopheline in Oaxaca, Mexico (Hoffmann and Samano 1938), Peru (Shannon 1930), Argentina (Shannon and Davis 1927), and Ecuador (Levi-Castillo 1945). We do not know if diapause occurs within the *An. pseudopunctipennis* populations during the wet season in southern Mexico. Hoffmann (1929) reported collecting overwintering larvae in springs from Central Mexico. Because he found 1st-instar larvae during cooler months, even with freezing temperatures, he agreed with the assessment by Shannon and Davis (1927) that some cool-weather breeding occurs because of favorable, warmer temperatures in seepage spring habitats.

Most wet season habitats containing *An. pseu-*

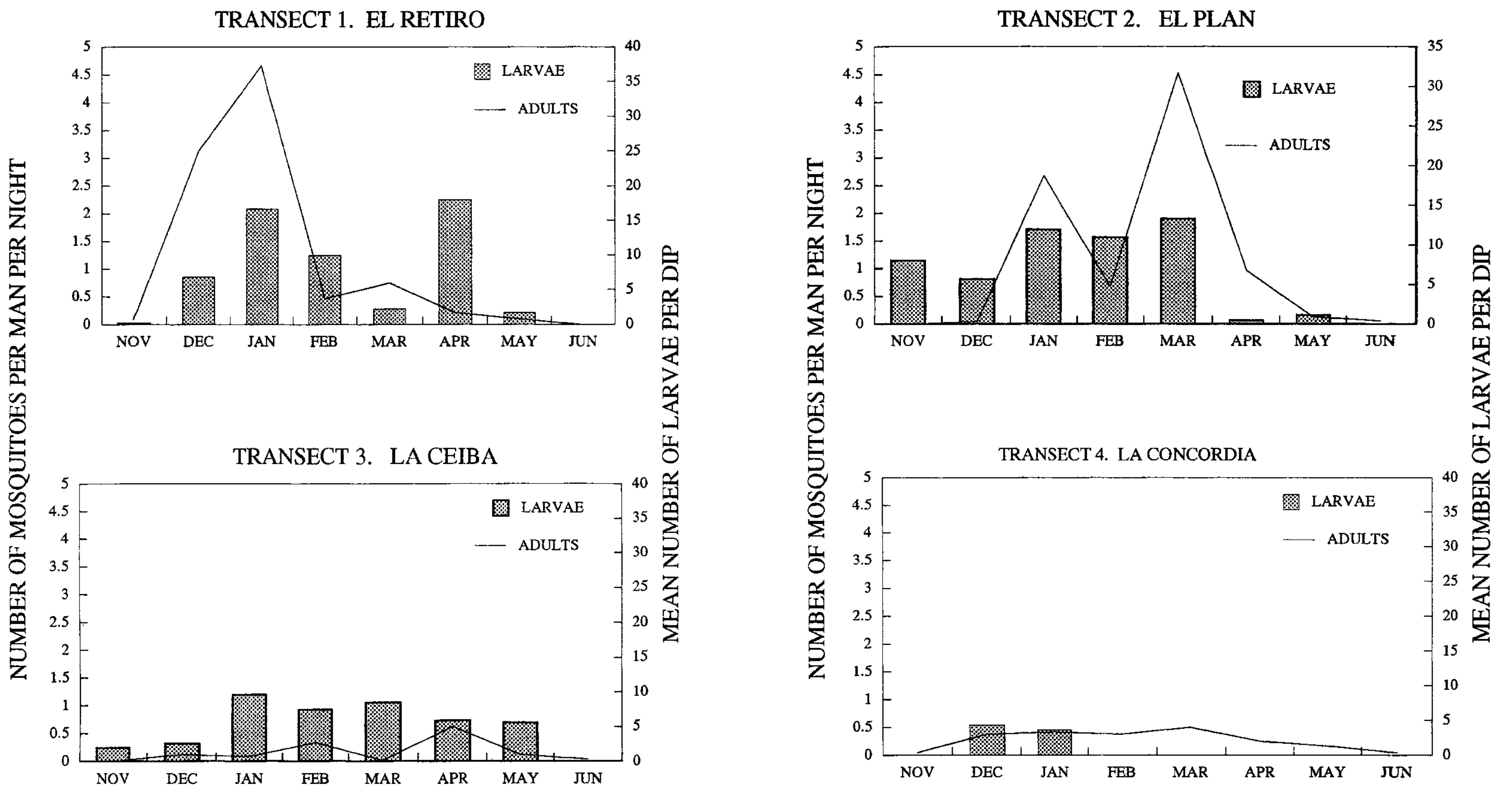

Fig. 3. Monthly densities of *Anopheles pseudopunctipennis* larvae and adults at 4 sites along the Coatan River in the foothills near Tapachula, Mexico, December 1990 to May 1991. Densities of adults were obtained by pooling data from all indoor and outdoor landing collections for each of 4 study villages. Densities of larvae are based on data from river transects at sites closest to each of the 4 villages.

dopunctipennis larvae also contained filamentous algae and other aquatic plants. Filamentous algae of the genera *Spirogyra* and *Oedogonium* (Chlorophyta) were found in 46.2% of the wet season habitats included in the sampling program and were uniformly present in the seepage spring habitats (Table 2). Moreover, filamentous algae grew densely in pools within transects along the Coatan River, with greatest abundance occurring during January to April. Savage et al. (1990) reported that the *An. pseudopunctipennis*–filamentous algae relationship could be used successfully to predict *An. pseudopunctipennis*-positive and -negative habitats. Furthermore, this phytoecological relationship has been reported for *An. pseudopunctipennis* throughout its geographical distribution from Mexico to South America (Shannon and Davis 1927, Aitken 1945, Hackett 1945). Hoffmann and Samano (1938) proposed that the algae served as shelter and food for the larvae and classified winter breeding sites in Oaxaca, Mexico, according to whether *Hydrodictyon* or *Spirogyra* algal species were most prevalent.

Savage et al. (1990) reported that *Heteranthera limosa,* a semiaquatic plant, was significantly associated with springs in which *An. pseudopunctipennis* larvae were collected. Our data indicated that floating plants and emergent grasses were strongly associated with some wet-season habitats. We believe that floating and emerged vegetation, either macrophytes or microphytes, might stimulate *An. pseudopunctipennis* females to select a particular oviposition site. Interestingly, larvae were seldom collected from wet-season habitats that contained little or no vegetation (e.g., gravel pits, lagoons, and a reservoir) (Table 1).

The transect method was useful for studying the dry-season breeding sites of *An. pseudopunctipennis* in the Coatan River. Increases in numbers of habitats and densities of larvae/pool occurred concurrently (Fig. 2). The increase in numbers of pools in the river bed was related to decreased rainfall. This is the expected situation, which seems to characterize the seasonal dynamics of *An. pseudopunctipennis* throughout its geographical range (Shannon 1930). All but one of the transects showed this relationship in numbers of pools with decreased rainfall. Higher numbers of breeding sites per transect were associated with villages located at less than 1 km from the Coatan River (e.g., El Retiro and El Plan). Although the transect at La Concordia was located 1 km from the river, it contained fewer pools during the dry season than during the wet season. This occurred because water is diverted from the river above El Retiro to a hydroelectric plant. The canal for diverting the water has been in use since 1966. The diversion of water provides a 16-km stretch of river with reduced water flow during the dry season. All transects and study villages, with the exception of La Concordia, are located along the river where water flow is reduced. Water is returned to the river about 500 m above the La Concordia transect, and results in increased volume and speed of river flow and in decreased numbers of pools in the La Concordia transect. Densities of adult and larval mosquitoes were equally low at La Concordia. This observation supports the idea that effective larval control can be achieved through environmental modifications or manipulations (e.g., draining pools and eliminating pool-forming depressions). These methods were successfully employed to control *An. pseudopunctipennis* in Ecuador (Levi-Castillo 1945).

When heavy rains began at the end of the dry season, the river pools containing filamentous algae and larvae were swept clean by increased river flow. When the rains begin there is a brief period when larvae are absent but adults are still abundant. However, after a few days the density of adult populations begins to decline as adult mortality outpaces the emergence of new adults. It seems likely that with the sudden disappearance of preferred oviposition sites, females begin selecting rain puddles as alternative sites for egg deposition. Intense egg-laying activity associated with dense adult populations in May (Fig. 1) and increased percentages of rain puddles containing larvae (15.2%) support this assessment (Table 1). Nevertheless, egg laying in rain puddles at the beginning of the wet season simply reflects selection of secondary oviposition sites when preferred habitats are not available.

The associations of *An. pseudopunctipennis* larvae with habitats containing filamentous algae were stronger in the dry season than in the wet season. The most prevalent genus of filamentous algae in the dry season was *Spirogyra* with *Cladophora, Closterium,* and *Oedogonium* being less frequently encountered. The microhabitats provided by the algae resulted in larval densities as high as 62 larvae/m^2 of surface area of filamentous algae. Range limits for seasonal mean numbers of larvae for the 4 transects were 16.7–53.9 larvae/m^2 of surface area of filamentous algae. The strong association of larvae with filamentous algae may provide potential for control through use of herbicides and genetically manipulated algae containing toxic bacteria crystals (e.g., *Bacillus thuringensis israelensis* and *B. sphaericus*) (World Health Organization 1987). Additionally, in the study area, dry-season malaria transmission by *An. pseudopunctipennis* should be amenable to control by larviciding. The small size of larval habitats (average size 2 m^2) and their focal distribution along river margins are factors favoring this approach to malaria control.

There was a positive correlation between numbers of larvae and numbers of adults collected at El Plan ($P < 0.05$). Correlations between numbers of immatures and adults were weak for the other 3 study sites; however, there was a general agreement in trends of immature and adult in populations (Fig. 3). The lack of statistically significant correlations between larvae and adult population densities could be related, in part, to the use of insecticides in villages to control adult populations. Unfortunately, insecticides for control of adults and larvae were not applied in a uniform manner at each of the study sites. For example, in El Retiro, DDT was sprayed on house walls in January 1991, whereas focal control, based on selectively spraying only those houses where malaria cases were previously reported (M. H. Rodriguez, unpublished data) was employed in El Plan during the same month. This difference in insecticide treatment probably had an impact on the densities of larvae and adult vectors in the 2 villages (Fig. 3). In the case of El Retiro, the applications of DDT to all house walls might have resulted in reduced larval population densities. Treatment of house walls with DDT has been reported to reduce larval densities in rice fields in Central Mexico (Gahan et al. 1949). The focal spraying of houses in El Plan probably affected a smaller segment of the house-visiting adults, and therefore had a smaller effect on larval populations.

Other factors accounting for discrepancies in densities of adult vs. larval populations in villages include variations in water flow and differences in distances of study villages from the Coatan River. A sudden release of water into the river in March, while the canal was under repair, eliminated many dry season pools in the transect at El Retiro, as seen in Fig. 3. On the other hand, high densities of larvae in La Ceiba transect did not correspond to the low densities of adult mosquitoes in the village, probably because the village was almost 2 km from the river. Although Levi-Castillo (1945) reported that the flight range of *An. pseudopunctipennis* in Ecuador is 3.6 km, our data suggested that the 2 km separating La Ceiba from the river is probably beyond easy flight range for most *An. pseudopunctipennis* adults.

As shown in this study, information on malaria vector larval ecology may provide supplementary knowledge to improve vector control strategies. Similarly, studies of landscape epidemiology should include investigations on vector bionomics, in order to thoroughly understand the associations of disease and the human environment.

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